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Research article

Winter soil temperature dependence of alpine plant distribution: Implications for anticipating vegetation changes under a warming climate[☆]



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ABSTRACT

The topographical heterogeneity of mountain landscapes and the associated species turnover over short distances should prompt us to examine the relationships between climate and mountain plant distribution at a much finer scale than is commonly done. Here, I focused on the root zone temperature experienced by low-stature perennial-dominated plant communities of temperate mountains, which are seasonally covered by snow. Based on the analysis of multi-annual recordings of ground temperatures across a broad spectrum of plant communities, I propose a habitat template using Growing Degree Days (GDD) and Freezing Degree Days (FDD). These two indices summarize soil thermal conditions experienced during the favorable and the unfavorable period for growth. This heuristic framework allows refining our working hypotheses on the range shifts of mountain plants in response to recent and future climate change. Regional trends in climate variables controlling GDD and FDD indicate that the combination of earlier snow melt-out and higher summer temperatures have led to an overall increase in GDD over the last decades. However the persistence of cold episodes in spring and in fall along with the shorter snow coverage suggest that the positive effect of an extended growing season might be counteracted by the detrimental effects of increasing FDD. I thus hypothesize (i) a local-scale, downward shift of plant species along mesotopographical gradients, with marked species infilling in sparsely vegetated, long-lasting snow patches that contain vacant niches and (ii) a watershed-scale upward shift of subalpine species inhabiting south-exposed grasslands and able to cope with moderate FDD. This perspective challenges the simplistic view of an overall range shift of mountain plants along elevational gradients and calls for the improvement of models of snow cover dynamics and root zone temperature to draw up realistic scenarios of mountain vegetation changes under a warmer climate.

1. Introduction

In arctic and temperate mountain ecosystems, snow cover dynamics not only determine the length of the favorable period for growth but also tightly control the duration and intensity of freezing temperatures that belowground, perennial tissues have to cope with during the unfavorable period. Shallow or inconsistent winter snowpack causes soil frosts that can persist over weeks or months in cold contexts and this has a long-term ecological significance for the distribution of overwintering organisms (Callaghan et al., 2011; Sutinen et al., 1999). A seasonal reduction of snow cover duration may expose tissues to damaging frosts in spring or in fall and several studies emphasized the impact of this climatic hazard on the performance of organisms (Abeli et al., 2012; Inouye, 2000; Kreyling, 2010; Pauli et al., 2013; Wipf et al.,

2009). The legacy of wintertime temperature regime on nutrient availability for plant growth during the following summer is also a key aspect of the functioning and the vegetation dynamics of snow-covered arctic and alpine ecosystems (Kreyling, 2010; Sturm et al., 2005). For example, increased microbial activity and higher N retention are observed in soils that benefit from the insulating effect of the snow (Baptist et al., 2010; Edwards et al., 2007) whereas freezing temperatures may favor the physical degradation of soil organic matter and the amount of inorganic nitrogen (Freppaz et al., 2008).

In mountain landscapes, thermal differentiations among nearby sites are related to the high topographical heterogeneity (Billings, 1973; Scherrer and Körner, 2010; Walker et al., 1993). During winter, these differences might be exacerbated by wind snow redistribution between sheltered sites where snow accumulates and exposed, wind-blown sites

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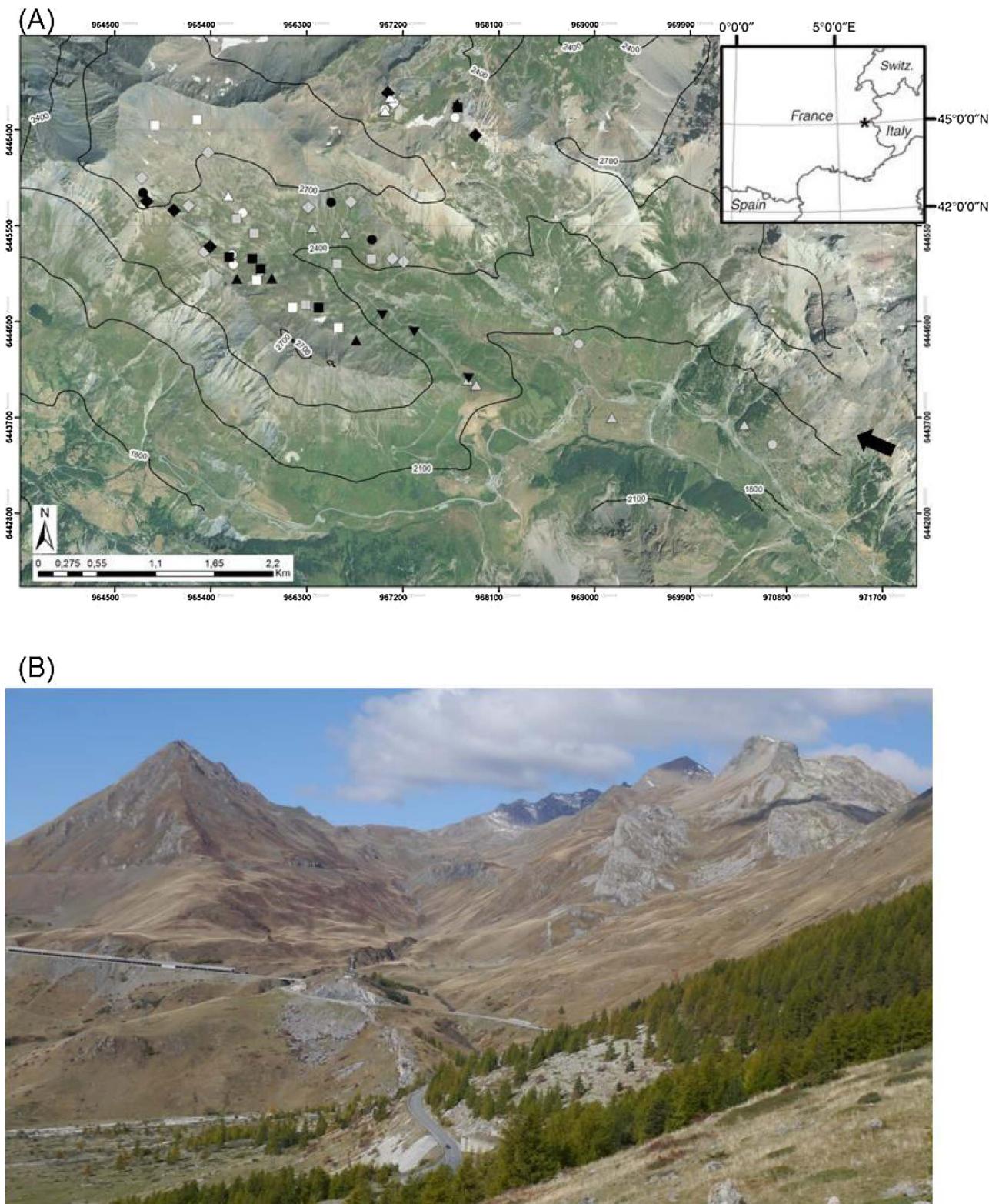


Fig. 1. Location of plots in the study area (A) and overview of the Roche Noire watershed (B). The arrow on the map indicates the position of the photographic shooting. The inset map shows the location of the study area in the French Alps. Symbols for plant communities follow Table 1.

where it is eroded (Essery and Pomeroy, 2004). As a result, highly contrasting soil temperature regimes are reported over mesotopographical gradients, i.e. ridge-to-snow bed gradients which typically represent a distance of a few meters (Baptist and Choler, 2008; Wundram et al., 2010). Consistent patterns of functional and taxonomic beta diversity and for different trophic levels have been documented

along these gradients (Heegaard, 2002; Kudo et al., 1999; Zinger et al., 2009). Consequently, the response of alpine plants to ongoing climatic change cannot be properly assessed if this patchiness of the thermal landscape is not properly understood (Graae et al., 2012). In line with this reasoning, a recent study pointed out that the magnitude of predicted change in temperature is relatively weak compared to what

plants would experience given a very short-distance range shift (Scherrer and Körner, 2011).

Current models that aim to project the distribution of high elevation species under a warmer climate suffer from the insufficient understanding and representation of the thermal envelopes of alpine plants. Fields of forcing variables are unavailable at the spatial scale that really matters for alpine plant life and the common practice of downscaling global climate gridded data is questionable because the local temperature experienced by low-stature plants is decoupled from atmospheric variables (Graae et al., 2012; Körner, 1999). If the local scale variation of key drivers of plant distribution is overlooked, projected distribution maps cannot be relevant. For example, Graae, (in press) emphasized the pivotal role of topographical complexity to understand how mountain plants will respond to climate change. Another weakness of current models pertains to the insufficient consideration of winter-time climate conditions because snow cover dynamics is poorly represented in these models (Carlson et al., 2013; Pradervand et al., 2014). Studies accounting for snow cover change on ecological processes, mainly focus on the impact of the first snow free day and the growing season length but winter soil temperature remains a missing dimension (Choler, 2015; Ernakovich et al., 2014; Heegaard, 2002). This is at odds with the recognition that winter conditions, and particularly winter soil temperature, are pivotal to capture biodiversity patterns and ecosystem functioning in snow-covered ecosystems (Pauli et al., 2013; Petty et al., 2015).

There is an increasing recognition that snow amount and duration have significantly declined in the Alps since the eighties in relation with a warmer climate (Beniston, 1997; Hantel et al., 2000; Hantel et al., 2012). This trend is clearly observed at intermediate elevations – typically below 1800 m (Hantel and Hirtl-Wielke, 2007) because of the high sensitivity of the snowpack to air temperature in this elevational range. Higher up, there remain large uncertainties essentially because inter-annual and regional variations in winter precipitation are poorly known (Beniston et al., 2003). The consequences of these snowline shifts on mountain vegetation have been mainly discussed from the viewpoint of its positive effect of the growing season length and its likely effect on the upward shift of plants (Carlson et al., 2015; Gottfried et al., 2011; Keller et al., 2005). However, a comprehensive assessment of the effects of snow cover changes on plant performance and distribution should also account for winter conditions and the interplay between snow cover, air temperature, and soil temperatures (Wheeler et al., 2014).

Miniature and standalone sensors enable a much more accurate picture of the thermal conditions really experienced by alpine plants compared to air temperature data provided by weather stations (Graae et al., 2012). Multi-annual soil temperature monitoring has been used to revisit some of the long-standing issues in the biogeography of cold ecosystems, such as the thermal features of the treeline (Körner and Paulsen, 2004; Körner et al., 2003). However studies examining multi-annual variations of summertime and wintertime thermal conditions and across a large range of mountain habitats are lacking. In this manuscript, I report analysis of a previously unpublished database of soil temperature regimes collected in a broad spectrum of above-forest habitats in the French Alps. I build upon this analysis to propose a thermal-based template for alpine plant distribution. More specifically, I show that (i) the duration and intensity of ground freezing temperature is complementary to the Growing Degree Days index to define the thermal niche of dominant alpine plants, (ii) the observed trends in regional climate and snow cover have significantly shifted these thermal domains over the past decades, and (iii) paying further attention to local soil temperature regimes, and especially during wintertime, is pivotal to move beyond the simplistic view of an overall upward shift of mountain plants under a warmer climate.

2. Materials and methods

2.1. Study area

Most of the data were collected in two sites locally known as *Roche Noire* and *Aravo* and located in the Grand Galibier Massif of the South-Western French Alps (Fig. 1). The Roche Noire site is a high elevation watershed with a predominant northwest to southeast orientation (Fig. 1). The main bedrock is represented by flysch sediments, called the ‘Flysch des Aiguilles d’Arves’ (Deharveng et al., 1987). The Aravo site consists of an inclined depression located between 2600 and 2650 m on calcareous shales (Fig. S1, Choler, 2005). A few additional plots were installed in the immediate vicinity of the Galibier pass (Fig. 1). In RON and ARA sites, soils are slightly acidic (pH between 5 and 6.5). Details on soil structure and chemistry are provided in table S1 of Zinger et al. (2011). The treeless vegetation is dominated by a mosaic of heathlands and productive subalpine grasslands in the lower part and by short stature alpine meadows, screes and rocks in the higher part. Based on previous vegetation surveys (Choler and Michalet, 2002) it is hypothesized that the subalpine to alpine ecotone is located between 2300 m and 2500 m depending on slope exposure. Sites are grazed extensively by cattle or sheep from June to September.

2.1.1. Field data

The study area lies between the Lautaret and Galibier passes and is well-known for its rich variety of bedrocks and landforms. Plots were only established on non-acidic sedimentary rocks with base-rich soils to ensure that the targeted plant communities are sharing a common species pool. Based on a regional field survey of vegetation (Choler and Michalet, 2002), I selected 56 plots to cover the most common vegetation types of the area. The sampling design was based on the physiognomy (vegetation cover, grassland vs. shrubland) and the presence/absence of dominant species. The resulting ten groups (Table 1) align well with the standard plant classification schemes of the Alps (Theurillat et al., 1994) and are representative of the subalpine, alpine and nival belts of this part of the French Alps.

Sites were equipped with miniaturized and standalone temperature data loggers (Hobo pendant UA, Onset Computer Corporation, Bourne, MA). Loggers were buried at 5 cm below ground level to monitor the near surface ground temperatures on an hourly basis. Most of the time series on which this analysis is based begin in 2007 and end in 2015. Vicissitudes of the monitoring program including battery issues and loss of sensors explain the numerous gaps in time series. Details on data availability per plot are shown in supplementary Fig. S1. Soil temperature monitoring and vegetation surveys are ongoing as part of a long-term program.

Near surface soil thermal conditions are representative of those experienced by the root system of perennial plants, which have a high density of roots in the topsoil layer. Root zone temperatures are highly responsive to snow cover dynamics (Harris et al., 2009; Schmid et al., 2012). Daily mean soil temperatures around 0 °C and showing no circadian thermal amplitude are indicative of the presence of a deep winter snowpack with efficient insulated effect. By contrast, negative daily mean soil temperatures generally occur in snow free conditions or when the snowpack is too shallow to buffer negative air temperatures. Negative soil temperature may eventually occur below a deep snowpack in the case of delayed snowfalls overtaking frozen soils.

2.1.2. Climate data

Time series of temperature, precipitation and snow height were provided by the SAFRAN-SURFEX/Crocus-MEPRA model chain (S2 M), hereafter SAFRAN–Crocus, developed by Météo France for the French Alps (Durand et al., 2009a,b; Vionnet et al., 2012). The model combines observed data from a network of weather stations and estimates from

Table 1

Main characteristics of the twelve surveyed plant communities. N is the number of plots per plant community. Mean (+/– 1 standard deviation) are given for elevation and bioclimatic variables (see Material and Methods for details).

Symbol	N	Dominant vascular plant	Elevation (m a.s.l.)	Plant cover range (%)	First Snow Free Day (Julian Day)	Growing Degree Days (°C)	Freezing Degree Days (°C)
●	3	Bromus erectus, Festuca laevigata	2062 (89)	70–90	80 (3)	1688 (117)	–108 (79)
▲	6	Patzkea paniculata	2201 (234)	90–100	116 (20)	1317 (181)	–4 (6)
●	3	Helictotrichon sedenense	2634 (136)	30–50	119 (16)	1082 (230)	–196 (235)
■	5	Carex myosuroides, Dryas octopetala	2538 (30)	50–70	132 (11)	1082 (143)	–536 (105)
■	5	Carex sempervirens, Trifolium alpinum	2499 (98)	70–90	147 (4)	985 (23)	–42 (58)
◆	5	Carex myosuroides, Sesleria coerulea	2670 (54)	70–90	141 (20)	1029 (168)	–322 (210)
▼	3	Vaccinium myrtillus, Vaccinium uliginosum	2292 (58)	80–100	145 (8)	867 (96)	–178 (166)
▲	5	Salix retusa, Salix reticulata	2562 (51)	40–60	148 (11)	802 (121)	–343 (211)
◆	9	Festuca violacea, Trifolium pratense	2615 (133)	30–60	160 (21)	1010 (144)	–39 (91)
△	3	Salix herbacea, Plantago alpina	2629 (2)	60–80	161 (5)	877 (106)	–13 (15)
○	6	Alchemilla pentaphyllea, Carex foetida	2581 (37)	90–100	167 (10)	762 (102)	0 (0)
□	5	Ranunculus glacialis, Poa distichophylla	2649 (165)	5–15	199 (15)	447 (143)	0 (0)

numerical weather forecasting models to provide hourly data of atmospheric parameters and snow amount and duration for 23 massifs of the French Alps. The model accounts for topographic features and climate variables are simulated for 300 m-wide elevational bands, aspect (seven orientations, and slope (flat, 20° and 40°). Because of its physical basis and the unavailability of forcing variables at the relevant scale, the model cannot represent mesotopographical variations of snow cover duration and amount. Therefore, model outputs were essentially used to provide a long-term temporal context of the regional climate and not to predict local thermal conditions. Climate re-analyses corresponding to the period 1959–2015 were extracted for different elevations and for the reference flat surface. The studied sites are located at the limit between the two climate massifs Thabor and Oisans. Because there were no significant differences when comparing long-term temperature and snow cover trends between these two massifs, figures given here are for the Oisans massif.

2.1.3. Data analysis

First the daily average of hourly values of soil temperature was calculated as follows

$$\text{Tavg} = 0.5 \times (\text{Tmin} + \text{Tmax})$$

where Tmin and Tmax are the minimum and maximum daily temperature, respectively.

Soil thermal conditions during the favorable period for growth were summarized by calculating a Growing Degree Days (GDD) index corresponding to the sum of average daily degrees above a given threshold (Z_{GDD}) following

$$\text{GDD} = \sum_i \text{Tavg}_i \text{ with } \text{Tavg}_i = 0 \text{ if } \text{Tavg}_i < Z_{\text{GDD}}$$

I used a threshold value of 1 °C instead of 0 °C because slightly positive daily averages can be observed even under a deep snowpack due to measurement errors of the sensor. Other Z_{GDD} values ranging from 1 °C to 5 °C were used without bringing any significant change to the comparative analysis of plots. GDD was estimated either by considering the whole set of days during which Tavg was above 1 °C or by setting a temporal limit at the end of August to restrict the analysis to the productive season. Again, this did not impact the main findings of this study. Noticeably, the GDD-based ranking of plots was not sensitive to this choice. This is mainly because the date of the first snow fall in autumn exhibits low variability among plots. On average, I found a

GDD decrease of 20% to 25% when the reduced time frame was used. Because this study mainly focused on spring and summer changes in thermal conditions, results are presented for the period ending on August 31st.

Soil thermal conditions during the unfavorable period were summarized using a Freezing Degree Days (FDD) index. FDD was calculated as the sum of average daily degrees below the threshold Z_{FDD} following

$$\text{FDD} = \sum_i \text{Tavg}_i \text{ with } \text{Tavg}_i = 0 \text{ if } \text{Tavg}_i > Z_{\text{FDD}}$$

Z_{FDD} was set to –1 °C for the reasons explained above. The computation of FDD follows the same logic used to estimate GDD, although a different threshold is used. FDD is used in climate science to capture both frost intensity and the length of the frost episodes for a given period (<https://nsidc.org/cryosphere/glossary/term/freezing-degree-days>). In this study, FDD was estimated on a yearly basis from the beginning of August of year $n-1$ to the end of July of year n to capture winter harshness.

3. Results and discussion

3.1. A bi-dimensional template for mountain plant thermal niches

The two year-long time series of root zone temperatures shown in Fig. 2 illustrate three contrasting soil thermal conditions. A comparison with daily minimum and maximum air temperature at 2500 m is also provided (Fig. 2A). A subalpine grassland dominated by the tall fescue *Patzkea paniculata* and located on gentle south-exposed slopes benefits from long and warm growing season (GDD around 2000 °C) and does not experience severe winter ground freezing temperatures (Fig. 2B). The slightly negative FDD in 2011–2012 is due to a very cold episode in spring 2012 – with minimum air temperatures below –10 °C (Fig. 2A) – at a time where the melting snowpack was shallow. At a higher elevation, a turf alpine meadow located on wind-blown ridges and dominated by *Carex myosuroides* copes with a reduced GDD (around 1200 °C) and most noticeably with intense and long-lasting ground freezing temperatures during winter (Fig. 2C). At the same elevation although in sheltered locations where snow accumulates, a short stature plant communities dominated by *Alchemilla pentaphyllea* is thermally insulated from the atmosphere all the winter long and shows FDD values equal to 0 (Fig. 2D). Though the growing season is much shorter than in the nearby *Carex myosuroides* community, it is significantly warmer (12.7 °C vs. 10.9 °C for the July average temperature). As a

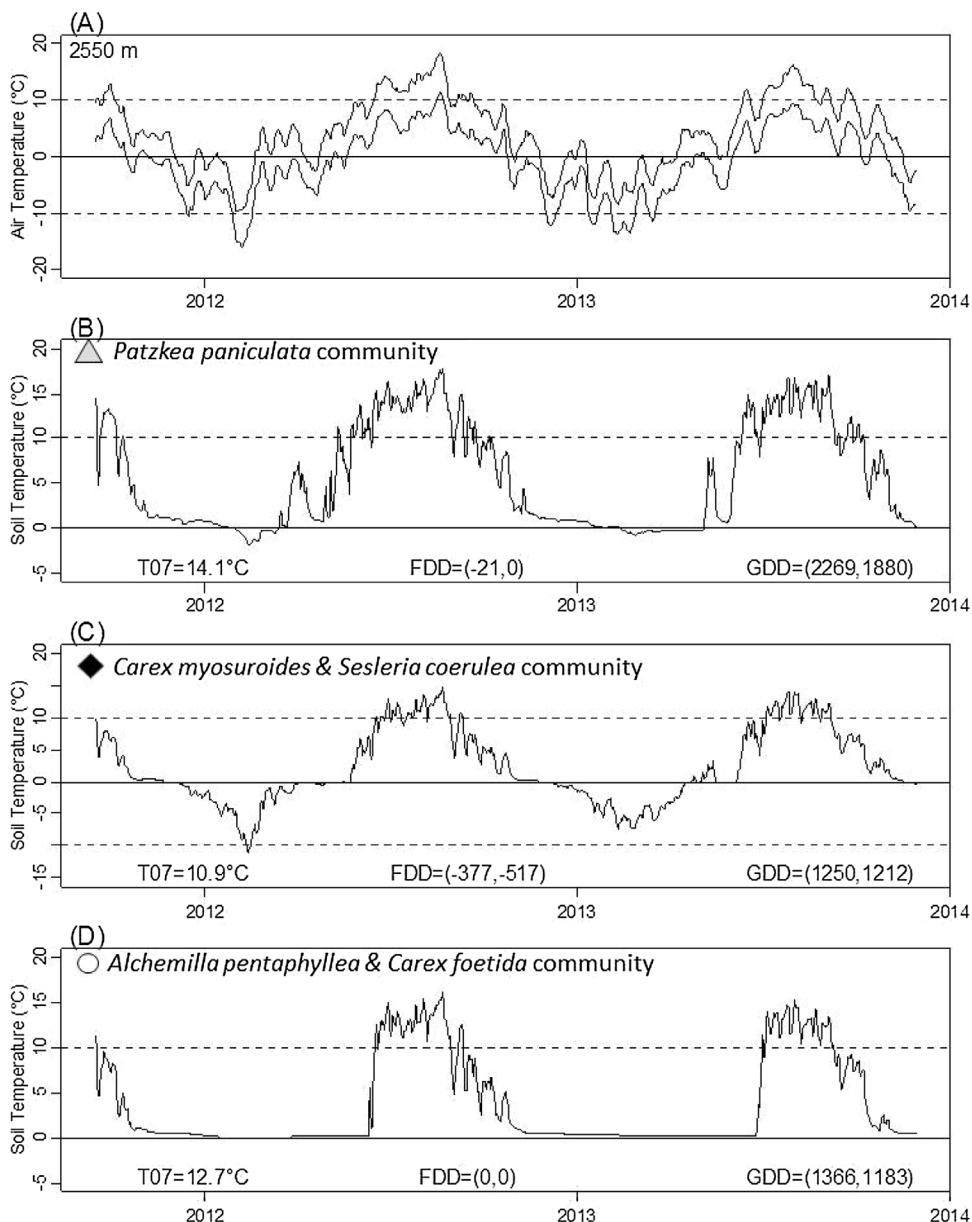


Fig. 2. Annual course of daily minimum and daily maximum air temperature (A) and daily average soil temperature in three contrasting plant communities (B, C, D). Freezing Degree Days (FDD), Growing Degree Days (GDD) and average July temperatures (T07) are given in brackets for each year. Air temperatures are from SAFRAN-SURFEX/Crocus-MEPRAS model chain (S2M) for the Oisans massif.

result, these two alpine sites exhibit similar GDD values. These three examples illustrate how GDD and FDD allow for characterization of thermal habitats of mountain vegetation along elevational and mesotopographical gradients.

Fig. 3 shows the relationships between GDD and FDD for all surveyed plots. Plots belonging to the same community are positioned closed to each other highlighting the ecological relevance of GDD and FDD for defining habitat niches. Plots that do not experience prolonged winter ground freezing, i.e. having FDD values between 0 and -100°C , are distributed along a gradient of GDD that ranges from subalpine grasslands to alpine snow beds. In the mid-range of this gradient, i.e. GDD values between 800°C and 1200°C , several plant communities experience low FDD values with the most severe conditions occurring in communities dominated by *Carex myosuroides* and *Dryas octopetala*. Overall, the variance within communities is higher for FDD than for GDD (Table 1 and Fig. 3B) and some community types can hardly be distinguished from one another on the sole basis of their thermal profiles. For example, there is a strong overlap in GDD and FDD between the sparsely vegetated communities dominated by *Helictotrichon sedens* and the turf meadow dominated by *C. myosuroides* and *Sesleria*

coerulea. Other ecological factors, such as the substrate stability for example, are to consider for further discriminating the habitat suitability of these dominant species. Further studies are also needed to examine the relevance of this thermal-based habitat template for species that do not account for a high proportion of the aboveground biomass, i.e. subordinates and transients *sensu* Grime (1998). Our previous studies have underlined the importance of biotic interactions to capture the distribution range of these species along elevational and mesotopographical gradients (Choler et al., 2001; Kikvidze et al., 2005). Anthelme et al. (2014) also emphasized the role of positive plant–plant interactions in the upward and downward range shift of alpine plants under a changing climate.

Finally, Fig. 3 also shows unrealized thermal conditions corresponding to the combination of low (or high) GDD and very negative FDD values. Late snow melting plots with low GDD values do not experience prolonged ground freezing because the only period during which this may happen is late fall–early winter in the event of delayed snowfalls. On the other side of the GDD gradient, low elevation plots may experience ground freezing just before or after the snowy period as illustrated in Fig. 2B. However this has never led to strongly negative

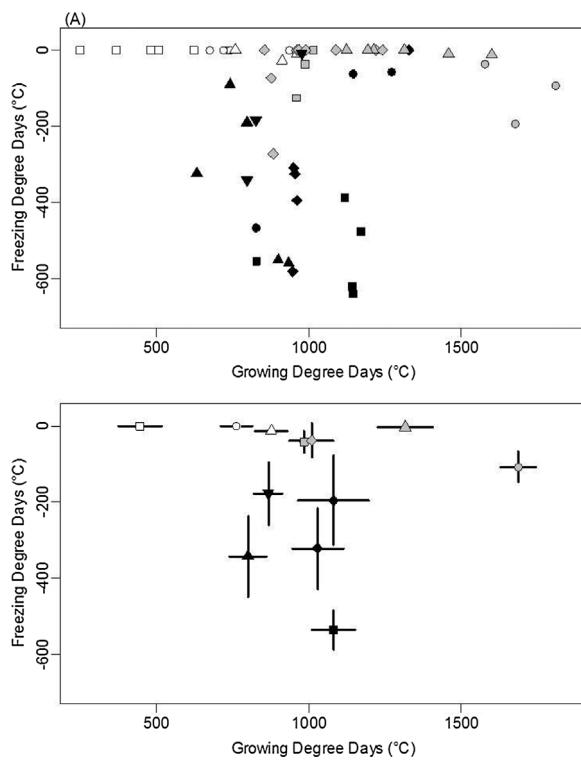


Fig. 3. Location of study plots in a bi-dimensional thermal-based habitat template. Time averages of GDD and FDD are shown for each plot (A) and for each plant community with ± 1 standard deviation (B). Symbols for plant communities follow Table 1.

FDD values likely because these plots experience rapid warming in the spring.

Overall, these results show that FDD and GDD are two key variables for a first-order habitat filtering of dominant mountain species. The relationship between these two variables delineates a thermal domain occupied by alpine plant communities and provides a heuristic framework to address the effect of climate change on plant community distribution as detailed below.

3.2. Regional climate change

Regional-scale trends of key climate variables controlling GDD and FDD are shown from 1959 onwards and for a reference elevation of 2400 m (Fig. 4). Yearly-based time series were derived from SAFRAN-Crocus re-analyses of air temperature and snow cover duration. The three last decades show a significant positive trend towards warmer summers (Fig. 4A). This is illustrated by examining the sum of average daily degrees above 0 °C for the period July-August. A breakpoint analysis identifies a shifting period in the late seventies – early eighties (Fig. 4A). Over the last thirty years this sum was 100 °C higher than it was during the period 1959–1978. Trends in the First Snow Free Day (FSFD) show similar patterns (Fig. 4B). From 1995 onwards, the average FSFD was the 150th Julian Day (30th of May) whereas it was two weeks later on (14th of June) in the preceding period. The snowy winters of the late seventies – early eighties (1978, 1979 and 1983) have never been observed since then, even if a high year-to-year variability has been noticed recently – see for example the contrast between year 2011 and year 2013. The shift towards low snow winters in the late eighties and the lack of significant trend since then have also been reported for the Swiss Alps (Marty, 2008). Finally, the sum of average daily degrees below –5 °C from April to June was used as a proxy for the duration and intensity of cold episodes in the spring. There have been several years with both cold springs and delayed FSFD in the eighties but overall this sum did not show any significant trend

over the period 1959–2016, despite the rise in temperatures (Fig. 4C).

To sum-up, the regional climate trend is marked by warmer and longer snowfree periods and by the persistence of cold events in spring. This means an increasing likelihood of exposure to frost events for early snow melting sites that do no benefit from the insulating effect of the snowpack. Using 37 years-long time series of climate data for the Swiss Alps, Wheeler et al. (2014) reached similar conclusions and pointed out this counterintuitive effect of global warming in mountainous environments. When considering species range shift under climate change, particular attention should thus be dedicated to the balance between the positive effect of increasing GDD (because of the longer and warmer snow free period) and the detrimental effect of a decreasing FDD (because of the increasing risk of ground freezing for soils insufficiently protected by snow). Accounting for these two dimensions of the thermal niche remains a challenge for Species Distribution Models. Predictions of alpine species distribution under climate change scenarios have commonly relied on spatially downscaled air temperatures (Engler et al., 2009). This approach is misleading as the actual temperature experienced by small stature plants strikingly deviates from the air temperature of weather station (Körner and Hiltbrunner, in this issue). In particular, the tight relationship between snow cover dynamics, soil temperature profiles and the distribution of dominant mountain plants has to be accounted for to draw up more realistic scenarios of vegetation changes under a warming climate. In the following section I propose a framework for making progress in this direction.

3.3. Implications for mountain plant distribution under a warming climate

First, I examined the likely effect of regional climate change on the FDD-GDD relationship. To be consistent with observed recent trends over the last three decades, I built up on a scenario with a 15 days shift in the snow melt-out date and a 100 °C increase in the sum of daily average degrees in July-August (Fig. 3). The earlier snow melt-out translates into additional degree days that were estimated using SAFRAN-Crocus times series of air temperature. For each half-month period, I calculated the sum of average daily degrees above 0 °C (hereafter positive degree days) and below –2 °C (hereafter negative degree days) (Fig. 5A). For example, a high-elevation snow bed located between 2400 m and 2700 m, and experiencing a snow melt-out the first of July instead of the 15th of July, would gain 131 positive degree days and no negative degree days. If the whole growing season is considered, this amount of extra degree days due to an advanced snow melting should be added to the 100 °C increase due to the warmer July and August. For a plot located at the same elevation but experiencing a snow melt-out the first of April instead of the 15th of April, the gain of positive degree days would only amount 10 °C and the negative degree days would amount –55 °C (Fig. 5A). As expected, the gain in positive degree days is higher in early summer than in the spring and it decreases with elevation due to the adiabatic lapse rate (Fig. 5A). The impact of an earlier snow melt-out on negative degree days is only noticeable early in the season and vanishes after mid-May (Fig. 5A).

These estimates of degree days based on air temperature need to be converted into GDD and FDD to be ecologically meaningful. As in previous studies (Zheng et al., 1993), I found a significant relationship between the daily average air temperature given by SAFRAN-Crocus and the measured daily average soil temperatures during the snow free period (supplementary Fig. 2A). Based on the estimated slope of 0.65, I hypothesized that an increase of 100 °C in positive degree days will contribute to a 65 °C degree increase in GDD. The effect of negative degree days on FDD is harder to quantify because it is highly dependent on the absence or presence of snow as well as the thermal resistance of the snowpack (Harris et al., 2009; Saccone et al., 2013). Empirical data shown in supplementary Fig. 2B indicate that daily minimum air temperature in the range –5 °C to –10 °C are generally associated with daily minimum soil temperatures below –2 °C. Although these data can

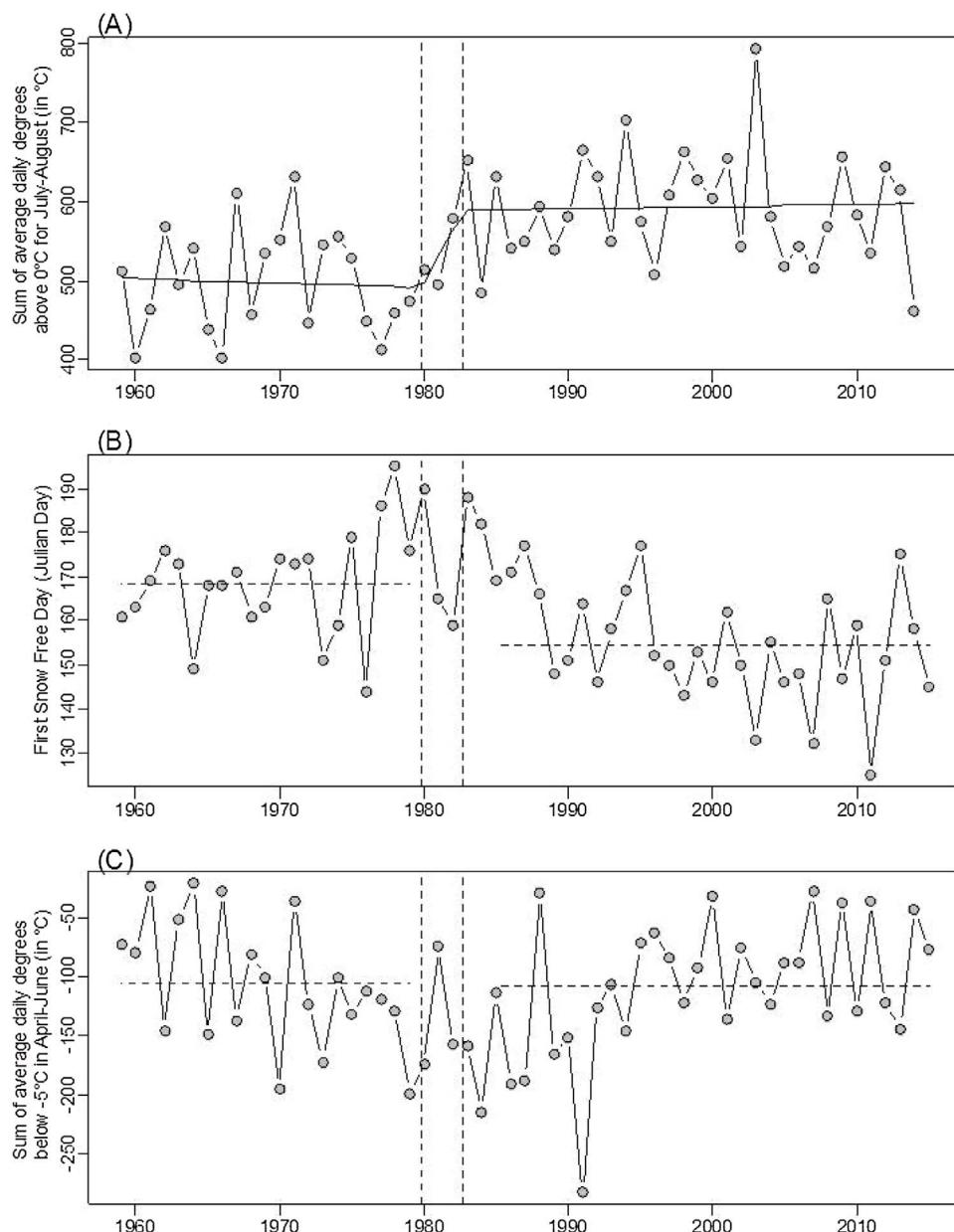


Fig. 4. Long-term trends of the sum of average daily degrees above 0 °C for the period July-August (A), the First Snow Free Day (FSFD in Julian Day) (B), and the sum of average daily degrees below -5 °C for the period April-June (C). Data are derived from the SAFRAN-SURFEX/Crocus-MEPRA model chain (S2 M) for the Oisans massif in the 2400 m–2700 m elevational band and for a flat surface. Regression lines in (A) result from a breakpoint analysis which identifies a period of regime shift from 1979 to 1985. Dotted lines in (B) and (C) represent the long-term averages before and after the regime shift.

be used to provisionally assess the cascading effects of cold air episodes on FDD, biophysical models of soil temperature accounting for snow cover, soil water content and vegetation cover are needed to improve our understanding of this relationship (Wang et al., 2008).

I built on this ensemble of observations and calculations to assess the likely shifts of thermal conditions experienced by the root zone of mountain ecosystems in response to ongoing climate changes (Fig. 5B). At first glance, it appears that calculated changes in GDD and FDD are of ecological significance. A GDD increase of 100 °C, which is a conservative estimate, represents 10% or even more of the average GDD value characterizing most of the plant communities (Table 1, Fig. 5B). It is also the average difference between *Carex sempervirens* communities and *Salix herbacea* communities (Table 1). For late snow melting plots, a GDD increase of more than 150 °C is plausible (Fig. 5) and means a spectacular change in thermal profiles. Taken together, these results suggest a significant amelioration of the thermal conditions experienced by mountain plant communities during the growing season. This might have triggered either a densification of plant coverage or species range shifts along elevational gradient and mesotopographical gradient

over the last decades. Unfortunately, there is no available long-term botanical survey to ascertain these changes in the studied area. However, a recent analysis of high-resolution Landsat images in the nearby Ecrins National Park points out to an overall greening of high elevation landscapes (Carlson et al., 2017). This result aligns with other reports on cold ecosystems showing an increasing vascular plant cover at the expense of bare ground over the last decades (Cannone and Pignatti, 2014; Elmendorf et al., 2012; Kullman, 2010; Rundqvist et al., 2011). At high elevation I hypothesize that the positive effect of increasing energy availability might be particularly pronounced in late snow melting habitats offering vacant niches. Aerial photographs dating back to the eighties show that nowadays sparsely vegetated patches in concave microsites were covered by snow even at the end of summer (supplementary Fig. 3). It is likely that the vascular plant cover has significantly increased in these habitats over the last decades with newly established plants coming from a local pool of pioneer species able to cope with low nutrient availability and substrate instability.

The positive effect of a longer growing season can be offset by the detrimental effect of cold-weather episodes if soils are insufficiently

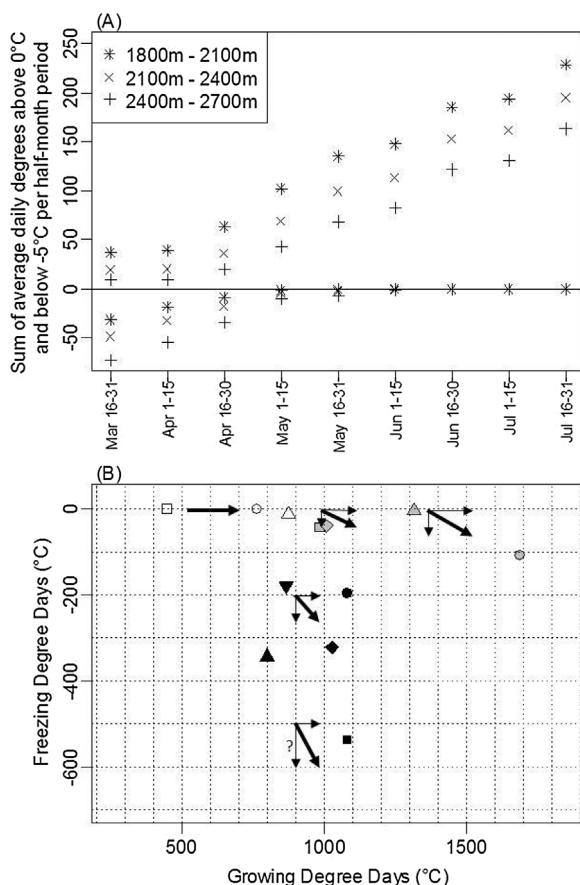


Fig. 5. (A) Sum of average daily degrees above 0°C and below -5°C for each half-month period between March and July. Values are averages over the past 30 years and are calculated using SAFRAN–Crocus air temperatures; (B) Scenario of GDD and FDD shifts in the bi-dimensional habitat template. The magnitude and direction of change indicated by the arrows are consistent with the observed trends in regional climate over the three last decades. Symbols for plant communities follow Table 1. See text for details.

protected by snow. Wipf & al. (2009) showed that this negative effect is species-specific with dominant species of early snow melting sites being the least sensitive to experimental reduction of snow cover. Here, I found that between-plot variation in FDD was high for all plant communities experiencing regular ground freezing temperatures during winter (Fig. 3B). This holds particularly true for communities dominated by *Carex myosuroides*, which are found in the most extreme thermal conditions. For these communities, a FDD decrease of 50 °C – a likely estimate given the scenario above – would be in the same order of magnitude as between-plot variation. By contrast, the same change in FDD may have a more significant impact for low elevation, south-exposed grasslands such as the *Patkea paniculata* communities (Fig. 5B). For these communities I hypothesize that the main beneficiaries of an increasing GDD will be those species able to cope with the associated decrease in FDD. By contrast, species unable to cope with this increased exposure to spring frosts may experience downslope range shift as pointed out by Lenoir et al., (2010). Species-specific long-term surveys or experimental manipulation of the snow cover duration should be conducted to test these hypotheses.

4. Conclusion & perspectives

Here I showed that the duration and intensity of ground freezing, which are summarized by the Freezing Degree Days index, exhibit marked variations along complex gradients of elevation and mesotopography and that this index, along with the Growing Degree Days index, represents a leading axis of habitat differentiation in the alpine

zone. Comparative studies are required to examine the relevance of this GDD-FDD habitat template for other alpine areas. In particular, these findings raise questions for alpine ecosystems that do not experience seasonal snow coverage such as the tropical alpine environments (Anthelme and Dangles, 2012; Rundel et al., 1994) or highly continental climates that exhibit reduced snow depth (Brun et al., 2013). The role of soil temperature as a driving factor of beta diversity patterns and ecosystem functioning along complex topographical gradients remains to be elucidated in these bioclimatic contexts.

An in-depth understanding of local bioclimatic change is needed to refine our current models of species distribution and anticipate species range shifts in response to global change (Lenoir and Svenning, 2015). In seasonally snow-covered alpine ecosystems, I point out that a better understanding of snow cover dynamics and root-zone temperature throughout the year is needed to draw up realistic scenarios of vegetation changes. There is a need to better quantifying the relationship between snow cover dynamics and root-zone temperatures. Predicting snowpack characteristics at an ecologically-relevant scale in complex terrain remains a challenge for physical-based models (Brun et al., 2013; Liston and Elder, 2006; Rankinen et al., 2004). Remote sensing approaches using high temporal and spatial resolution are valuable for quantifying snow cover duration at a regional scale (Dedieu et al., 2016; Kivinen et al., 2012). Complementary developments in laser altimetry and infra-red thermometry are also promising to mapping snow depth and surface temperature in mountain catchments (Deems et al., 2013; Revuelto et al., 2014; Scherrer and Körner, 2010). Using these data to calibrate high-resolution models of soil temperatures will provide new opportunities to quantify the thermal niche of alpine plants.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ppees.2017.11.002>.

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